

EVOLUTION OF PREY-CARRYING MECHANISMS IN DIGGER WASPS:  
POSSIBLE ROLE OF A FUNCTIONAL LINK BETWEEN PREY-PARALYZING  
AND CARRYING STUDIED IN *OXYBELUS UNIGLUMIS*  
(HYMENOPTERA, SPHECIDAE, CRABRONINAE)

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*Some Oxybelus digger wasps (Crabroninae) carry their fly prey on the sting. A study of Oxybelus uniglumis wasps, in controlled laboratory units, using observational methods, ciné-photo analysis and macroscopical study of the sting punctures, revealed that the number of stings (usually one only) and their precise location, just behind one foreleg, are remarkably constant. The wasp usually does not pull out the sting after having paralyzed the prey. Re-stinging occurs if the prey-carrying wasp is artificially or accidentally separated from its prey. It is not known, however, whether venom is also re-injected. This suggests that such a very specialized prey-carrying method might be derived from prey-stinging, paralyzing behaviour. A great fixity of prey-stinging methods might therefore favour, even be a prerequisite to, the evolution of even more specialized prey-carrying methods, based on the use of a modified abdomen tip (e.g. "ant-clamps", in the philanthine wasps Clypeadon). As pointed out by Evans (1977), the latter however requires a great degree of prey-specificity, because of the precise anatomical adjustments that are required, between wasp and prey. This might be counterproductive in Oxybelus wasps that prey on a great variety of flies. Some other Crabroninae and Philanthinae also sting their prey only once, in general, and also behind one foreleg. This peculiar prey-stinging behaviour is therefore widespread and rather constant, across genera and even some subfamilies. In contrast, a number of Orthoptera hunters usually sting their large and powerful prey repeatedly (often four times) and hunters of large caterpillars deliver an even greater number of stings, on the average.*

*Certaines guêpes du genre Oxybelus (Crabroninae) transportent leurs proies, des diptères variés, au bout de l'aiguillon. Une analyse photo-cinématographique en laboratoire et l'étude macroscopique des traces laissées par l'aiguillon, révèlent que le nombre de piqûres infligées (une seule en général) et leur distribution, sur la membrane molle à la base et à l'arrière d'une des pattes antérieures, varient peu chez Oxybelus uniglumis. Après la piqûre, la guêpe laisse simplement l'aiguillon en place dans la proie. En cas de séparation accidentelle ou expérimentale, durant le transport, la guêpe pique à nouveau sa proie. Il n'a pas été possible de savoir si la guêpe renouvelle ou non l'injection de venin. Dans la première éventualité le comportement serait équivalent à la piqûre qui suit la capture de la proie; dans la seconde, il s'agirait seulement de "ré-empaler" la proie et de reprendre le transport interrompu. Il semblerait donc que cette méthode de transport très particulière ait évolué à partir du comportement de piqûre (paralyse) de la proie. La remarquable constance de ce dernier comportement pourrait bien avoir favorisé aussi l'évolution d'une méthode de transport encore plus spécialisée, qui s'est accompagnée d'une modification anatomique de l'extrémité abdominale de la guêpe, sous la forme d'une "pince préhensile" (Clypeadon, Philanthinae). Evans (1977) a montré qu'en raison des ajustements anatomiques précis qui sont requis, cette dernière méthode exige une sélection étroite des proies, des fourmis. Cette méthode serait donc peu compatible avec la biologie présente des Oxybèles, qui chassent des diptères extrêmement variés. D'autres Crabroninae et Philanthinae piquent également leur proie une seule fois, à la base et à l'arrière d'une patte antérieure. La constance de ce comportement n'est donc pas restreinte aux Oxybèles mais s'étend à des genres entiers et même des sous-familles différentes, attestant ainsi la stabilité de cette méthode. Beaucoup de chasseurs d'Orthoptères, par contre, infligent à leur proie volumineuse et vigoureuse une série de piqûres successives (souvent au nombre de quatre). Les chasseurs de grosses chenilles vont encore plus loin dans le nombre moyen des piqûres infligées à la proie.*

## INTRODUCTION

Prey-carrying on the sting, by some *Oxybelus* wasps (Crabroninae) has been well documented and described, following an earlier period of rather contradictory reports. Use of leg(s), a more orthodox prey-carrying method, is also known from *Oxybelus* wasps, even some of the species that also carry the prey on the sting. *Clypeadon* wasps (Philanthinae) go even one step further and carry their ant-prey on the tip of their modified abdomen, transformed into a special organ ("ant-clamp": Evans 1962a). The latter author (1962b) hypothesized that evolution of prey-carrying mechanisms is probably related, at least in part, with a reduction in the incidence of parasitism by flies. Some miltogrammine flies, like *Senotainia*, for instance, oviposit on the prey before storage and can take advantage of any delay in nest re-opening. Carrying the prey on the sting or with an abdominal clamp frees all leg pairs and the mandibles, and therefore promotes a speedy nest re-opening and efficient digging activities. Also this frees the wasp from having to temporarily drop the prey and leave it unattended, while re-opening the temporarily closed burrow.

Some evidence is presented in this paper, suggesting that such specialized abdominal methods of prey-carrying might have derived from prey-stinging methods. A strong functional link between these two activities is clearly indicated in *Oxybelus* wasps.

## BACKGROUND INFORMATION

Conflicting reports in the early literature obscured the issue of prey-capture and carrying found in some *Oxybelus* wasps. Stinging was even sometimes discounted, the short abdomen of the wasp being considered too rigid! (Verhoeff, cited by Ferton 1923, p. 171, and also Ashmead 1894, cited by the Peckhams 1905, p. 79). On the basis of thoracic wounds found on the prey, *Oxybelus* wasps were also believed to crush their prey with the mandibles rather than to sting them into paralysis or death, like most other digger wasps do (e.g. references above). Even after prey-stinging had been discovered or suspected, much uncertainty remained as to what part(s) of the body was (were) stung: neck region (e.g. Sickmann 1883, p. 81, cited by Hamm and Richards 1930, p. 115: "the lower surface of the neck"; Chevalier 1926: *O. uniglumis*; Crèvecoeur 1929, p. 362: *O. bipunctatus*), ventral side of the thorax (e.g. Ferton 1923, pp. 172–173: *O. melancholicus*: "near the throat"; Parker 1915, pp. 74–75: *O. uniglumis quadrinotatus*), central area of the thorax underside (e.g. Tsuneki 1969, p. 14: *O. strandi* Yasumatsu), thin anterior part of the thorax underside, sometimes a little on one side of the middle line (e.g. Adlerz 1903, cited by Hamm and Richards 1930, p. 115). A few authors, however (e.g. Olberg 1959) clearly indicate, on the basis of direct observation and/or excellent photo documents, that the flies (taken by *O. subulatus*: Peckham *et al.* 1973) were . . . "impaled through the forecoxal corium". In many cases, however, only a few observations were made, no study of punctures done and no quantification attempted. Furthermore, initial prey capture and stinging were seldom witnessed, in natural conditions, reports being based essentially on re-stinging (or re-impaling?) often obtained by artificially separating the prey from the wasp, or observed after accidental separation (e.g. after copulation: Peckman *et al.* 1973, p. 654). No distinction was made between initial stinging and re-stinging, the similarities or differences between them. Some authors, however, either observed or postulated a link between prey-stinging and subsequent carriage, since the wasp did not pull out the sting after stinging (e.g. Adlerz 1903, cited by Hamm and Richards 1930, p. 155; Ferton 1923, p. 172: *O. melancholicus*; Williams 1936, p. 2: *O. u. 4-notatus*; Tsuneki 1969, p. 14: *O. strandi*). Bischoff (1927, p. 367), on the other hand, was aware of the evolutionary implications and considered this prey-carrying method as probably derived from stinging. He also thought that

a considerable delay in sting withdrawal, found in many digger wasps, could foreshadow use of the sting for carrying.

The present study, conducted in fully controlled laboratory conditions, represents an attempt to clarify some of these ambiguities and quantify to some extent various parameters of this behaviour.

Prey-carrying on the sting is apparently restricted to some Crabroninae (Evans 1962a, p. 256) and has been reported from several *Oxybelus* species such as *uniglumis* (L.) (1), *u. quadrinotatus* Say (2), *subulatus* Robertson (3), *bipunctatus* Olivier (4), *14-notatus* Jurine (5), *melancholicus*<sup>1</sup> Chevrier (6) (for instance by Fabre, in Ashmead, cited by Parker 1915, p. 74; by Parker 1915, for 2; by Ferton 1902, pp. 516–517, for 5; by Ferton 1923, p. 172, for 6; by Strandtmann 1945, p. 313, for 2; by Williams 1936, p. 2, for 2, etc.). It has also been reported from *Crossocerus elongatulus* (Van der Linden), a Crabronini, not an Oxybelini, by Nielsen (1933, p. 272).

### MATERIAL AND METHODS

*Oxybelus uniglumis*<sup>2</sup> was selected, since it is a common widespread Holarctic wasp, ranging from Europe, Mongolia, throughout North America probably via the Northwest Passage (Bohart and Schlinger 1957) into Mexico (Muesebeck *et al.* 1951; loc. cit. above; Krombein *et al.* 1958; Bohart and Menke 1976). It is found as far North as the Northwest Territories, Canada (Steiner 1973) and Alaska, U.S.A. (Elliott and Kurczewski 1973). Furthermore it preys on rather common flies, especially Muscoidea, including house flies, and its biology is relatively well known, from many different geographical locations (see for instance the above references and also: Peckham and Peckham 1898, 1905; Ferton 1902, 1910, 1923; Parker 1915; Hamm and Richards 1930, which summarize earlier work; Nielson 1933, Williams 1936; Nuorteva 1945; Strandtmann 1945; Krombein 1948, 1956; Guiglia 1953 with an extensive bibliography; Tsuneki 1969; Evans 1970 etc.). More recently Peckham *et al.* (1973) added much information on *Oxybelus* biology. Excellent photos can be found in the latter reference and also in Olberg (1959, pp. 376–390). These helped clarify some aspects discussed in this paper and provided much needed comparative material.

General methods of rearing digger wasps, designed by the author, are described elsewhere (Steiner 1965). Improved, collapsible and portable controlled units, kept inside a laboratory trailer, were used. The trailer was parked inside the study area, in central Oregon, U.S.A. Two individual wasps (Nos. 1019 and 1207) were intensively studied over an extended period of time: wasp 1019 was captured on May 25, 1977, N.E. of Bend, Deschutes Co., Oregon, and kept in captivity until July 5, when it was accidentally killed; wasp 1207 was captured near Cove Palisades, Jefferson Co., on July 11, 1977 and kept until August 2, when observations were discontinued. The study covered a total of about 157 hours of observations distributed over a period of 25 observation days. The average duration of daily observations is therefore 6h20min: for wasp 1019 the total was 94 hours for 16 observation days, and the daily average 5h53min; for wasp 1207 the total was 63h30min for nine observation days, and the daily average 7h10min. Additional observations on prey hunting, stinging and on nesting behaviour will be published elsewhere (Steiner, in prep). Soil for nesting was available to the caged wasps *ad libitum*, as well as food (honey) and water. Prey consisting of various flies, mostly small muscids, were not given *ad libitum* but only at times when subsequent uninterrupted observation was possible so that all prey-related behaviour could be controlled and recorded. Whenever possible, the flies were also given at a time of day when the wasps were most likely to start prey hunting and storage, as assessed by the end of nest digging and subsequent temporary closure with a sand plug. The wasp then usually undertook "searching trips" for flies.

1. *victor* Lefebv. in Bohart and Menke's recent book (1976, p. 370).

2. Bohart and Menke 1976, p. 370; *O. u. quadrinotatus* in the Synoptic Catalog (Muesebeck *et al.* 1951; Krombein *et al.* 1958).

Sometimes, however, time of presentation of prey deviated considerably from the time of spontaneous occurrence of hunting. Usually the wasps then readjusted their nesting cycles accordingly and within rather wide limits. This fully reveals the remarkable plasticity of nesting cycles at least in terms of temporal distribution over the day and from day to day (see also Steiner 1976 for *Liris* wasps). Consequently in the latter case observed nesting cycles represented a dynamic compromise between repeatable daily cyclical events and non-rhythmical modifying factors depending on the time of prey presentation, etc. Daily activities were much more regular, repeatable in a previous study when prey were available to *Liris nigra* wasps *ad libitum* throughout the day (Steiner 1962).

## RESULTS

### Observational Results

In contrast to natural conditions, initial prey capture, followed by prey paralyzing (stinging) was consistently and frequently observed in captivity (Fig. 1), under ideal observation conditions, day after day. The wasp was always curled around the anterior end of the fly, very close to the head, and the sting was always inserted ventrally on the thin membrane just behind one of the forelegs (Fig. 2, stippled area; L = foreleg bases, coxae). This is the same body site as reported by Peckham *et al.* (1973) for *O. subulatus*. Without pulling out the sting, the wasp then carried the impaled and paralyzed prey to the nest. This clearly confirms, or establishes, the functional link between prey-paralyzing and carrying. Both activities are more or less inseparable here, contrary to re-stinging, which is ambiguous since it is divorced from initial prey capture. There was no exception for such a linkage in 65 cases studied. Furthermore, initial stinging is indistinguishable from re-stinging following artificial wasp prey separation (analyzed later), including the point of insertion of the sting (large dots, Fig. 2) which is the same. The question of a possible difference if no venom is injected during re-stinging (re-impaling only?) could not be settled. Remarkably, the tip of the sting of some *Oxybelus* wasps is barbed. This probably reduces the chances of accidental loss of the carried prey. In contrast, most or all other digger wasps have a smooth sting (Evans 1962b).

A detailed study of prey hunting and paralyzing (Steiner, in prep.), that involves a minimum of 89 stings (53 from wasp 1019 and 36 from wasp 1207), fully confirmed this constancy and also established the following facts: 1) overwhelmingly, only one single sting is given initially to the prey: from 65 flies used for the prey paralyzing/carrying study, only a maximum of nine had possibly received more than one sting (see Tables 1 and 2). Instant and almost total paralysis of the fly results, except for twitching of leg tips, occasional abdomen pulsations and proboscis extensions and flexions, as also reported by various authors. Clearly the flies are not instantly killed, but deeply paralyzed. All reactions usually disappear within very few days; 2) the single point of insertion of the sting used for both prey paralyzing and carrying, was remarkably constant. It was, without exception, the thin membrane that forms the articulation behind the foreleg (Fig. 2, stippled areas). Even precise location of the punctures on this membrane varied little, as confirmed by a thorough study and mapping of the traces left by the sting, using, as in previous studies, a grid with coordinates (Fig. 2). Punctures become clearly visible as necrosis of the damaged tissues progresses over a period of one to several days (Steiner 1962, 1976). On Fig. 2, on each side, the large dot is the point of greatest sting concentration, and the small arrows, radiating from it, indicate the major directions and maximum range of scattering around this point. It might be worth mentioning that this is the only membrane immediately adjacent to the single thoracic mass of fused ganglia.

An occasional sting on the membrane of the neck region (horizontally hatched area on Fig. 2) cannot be ruled out, since detection of punctures on this rather folded membrane is

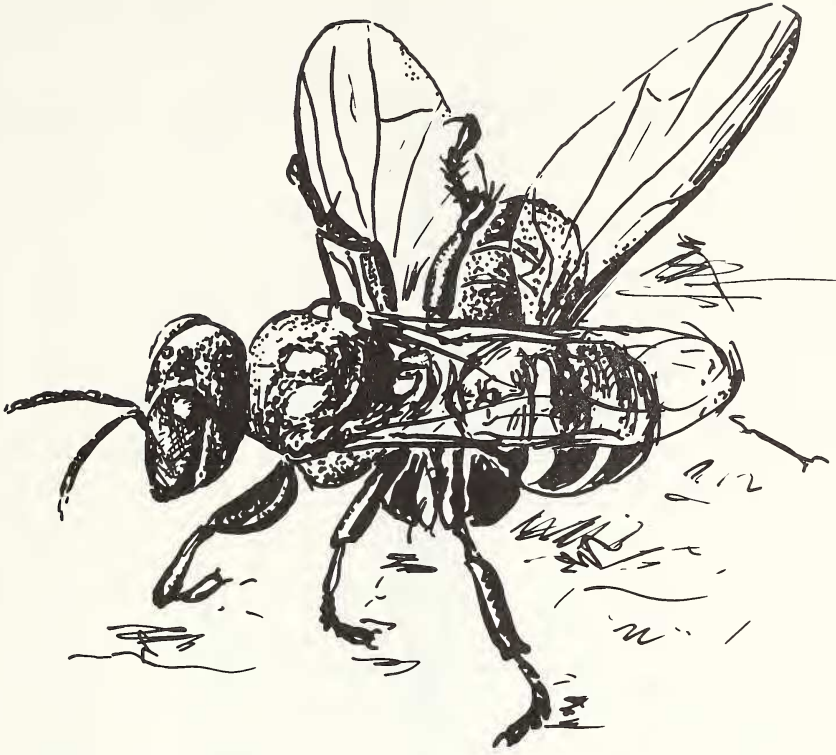


Fig. 1. Prey stinging (paralyzing) posture assumed by an *Oxybelus uniglumis quadrinotatus* wasp, later followed by prey carrying on the sting (Fig. 3A to C). Note how the wasp holds one wing of the prey with the claws. Drawn from a (somewhat out of focus) photo taken with electronic flash at approximately 1/2000 sec.

very difficult or impossible. No case of insertion of the sting on this membrane was, however, directly observed, neither for paralyzing nor for carrying.

3) Furthermore, in the few cases where both the stinging and carrying side could be recorded by direct observation (and/or photographically = \* in Tables 1 and 2), they coincided (see Tables 1 and 2, col. 2 and 3). The wasp abdomen tip was always inserted behind the same foreleg, left or right, that was also slightly tilted upwards, when compared with the side of the other foreleg, not used for sting insertion (e.g. Fig. 3A to 3C and Fig. 4). No exception to this uplifting of the carrying side was found in the 65 cases studied. When only the carrying side (left or right) had been recorded, the stinging side used for paralyzing having been missed, a careful subsequent study usually revealed the presence of only one puncture on one of the many soft membranes of the fly (Tables 1 and 2, col. 4). This is therefore indirect proof that again, paralyzing and subsequent carrying coincided. This also established unequivocally that there is indeed no separate "impaling" by re-insertion with new puncture, that would be distinct from initial prey paralyzing (stinging). One would then find consistently two different punctures, either at the rear of the same foreleg base, if paralyzing and carrying sides were consistently the same, but re-insertion was involved, or else one would find more or less at random the punctures both on one side or one on each leg base if paralyzing and carrying sides were not consistently correlated. The correlations found were highly significant, using as null hypothesis a random distribution of stinging side, carrying side, and puncture side, assumed to

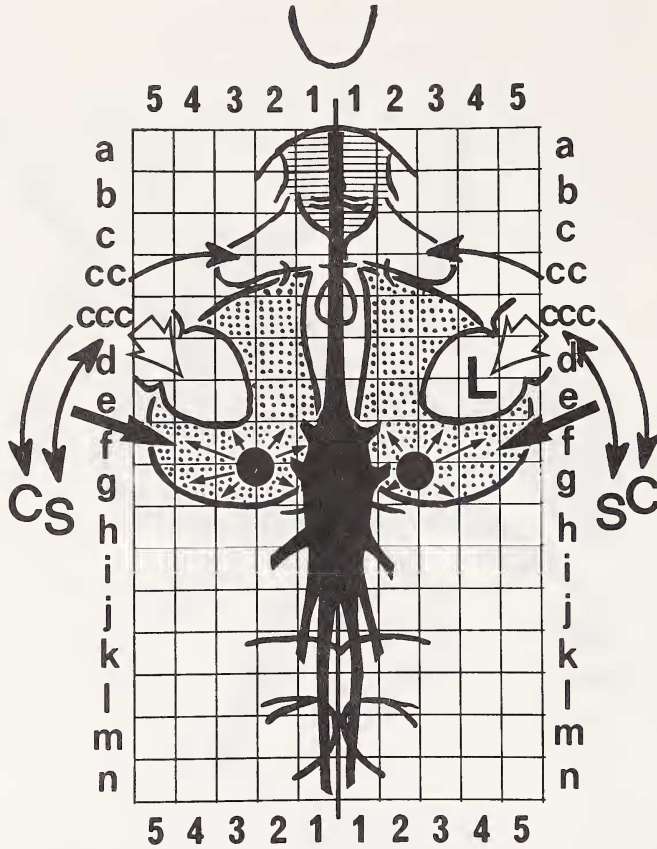


Fig. 2. Enlarged ventral view of fly foreleg bases, with superimposed grid, showing, for each side, soft membrane used for sting insertion (stippled area) used both for paralyzing and carrying, point of maximum puncture concentration (cumulative study of about 89 stings): large dot, major directions and ranges of dispersion around this point (small arrows radiating from large dot), average direction of stinging (large solid arrow) and of prey carrying (open arrow) and corresponding ranges of variation (curved arrows: S and C respectively). Position of the single mass of fused thoracic (and some abdominal) ganglia is shown in solid black, as seen by transparency. Horizontally hatched area represents another thin membrane (throat area) apparently not used for stinging/carrying. L = foreleg bases (coxae).

be independent for each individual case (no coincidence, equal expected frequencies): for wasp 1019 (Table 1) in 35 cases out of a total of 37, the observed (or photo recorded) prey carrying side and the subsequently found puncture side coincided ( $X^2 = 29.43$ ;  $p < .001$ ) and for wasp 1207 the proportion was 27 out of 28 ( $X^2 = 14.14$ ;  $p < .001$ ). Similarly, the proportions of cases where only one sting was found on the carrying side and none on the other side were 33 out of 37 for wasp 1019 ( $X^2 = 22.73$ ;  $p < .001$ ) and 23 out of 28 for wasp 1207 ( $X^2 = 11.57$ ;  $p < .001$ ).<sup>3</sup> The coordinates of the stinging-carrying punctures are given in the 6th column of the tables.

*Remarks.* — 1. Even the few exceptions to the above correlations or doubtful cases are ambiguous and do not necessarily mean that occasionally the functional link between paralyzing and carrying was in default: thus on flies 1131, 1168 (Table 1) and 1284 (Table 2) a second puncture was found on the other foreleg base of the prey too. This can mean one of two things, a) that the prey had been paralyzed by sting insertion on one side and the sting re-inserted subsequently for carrying on the other side (paralyzing and carrying sides different) or, b) that the prey had already been stung and carried on one side once before the observation recorded on the table was made, but the fly had been dropped on the ground before storage

3.  $X^2$  has been computed for each pair of relations by using the formula  $X^2 = \frac{n \sum (o_i - e_i)^2}{\sum e_i}$ , for equal expected values (Freund 1962); for wasp 1019,  $E = 18.5$  and for wasp 1207,  $E = 14$ , with  $df = 1$ .

Table 1. (Wasp 1019). Relations between stinging and carrying side of prey (col. 2 and 3) and side where puncture(s) found subsequently (col. 4), including number of punctures (col. 5) and possible effects of chronological order. (Explanations in text). (photo records: \*). L=left, R=right

Prey reference Number	Observed stinging side	Observed carrying uplifted side	Puncture side	Number of punctures	Puncture coordinates (rf. Fig. 2)	Date (1977)
1	2	3	4	5	6	7
1078		L	L	1	g2(L)	June 21
1085		R*	R	1	g2(R)	June 22
1086		R*	R	1	g3(R)	"
1087		L*	L	1	f2(L)	"
1089	R	R	R	1	f3(R)	"
1090		L*	L	1	f3(L)	"
1091	L	L*	L	1	f3(L)	"
1092		R*	R	1	g3(R)	"
1095		R*	R	1	f3(R)	June 23
1098		R*	R	1	f3(R)	"
1101		R*	R		f4(R),	"
				2	g2(R)	"
1102	L	L*	L	1	g3(L)	"
1121	R	R	R	1	g3(R)	June 27
1122		R	R	1	g3(R)	"
1123		R	R	1	g3(R)	"
1124		L	L	2	g2(L)	"
1125		L	L	1	g2(L)	June 28
1126		R	R	1	g4(R)	"
1127		L	L	1	f2(L)	"
1128		L	L	1	f2(L)	"
1130		L	L	1	f2(L)	"
1131		R	R+L	2	g3(L),	"
					f4(L)	"
1133	L	L	L	1	f4(L)	"
1134	R	R	R	1	f3(R)	"
1135		L	L	1	g2(L)	"
1136	L	L	L	1	f2(L)	"
1137		L	L	1	f4(L)	"
1139		R	R	1	f4(R)	"
1158		L	L	1	g3(L)	June 30
1159		L	L	1	f2(L)	"
1164		L*	L	1	f4(L)	July 1
1165		R*	R	1	g3(R)	"
1166	R	R*	R	1	f3(R)	"
1167		R*	R	1	g2(R)	"
1168		R*	R+L	2	f3(R),	"
					f3(L)	"
1172		R*	R	1	f3(R)	July 2
1173		L	L	1	?	"

Totals:

Prey: 37

coincid.:

non coincid.:

(possibly or doubtful)

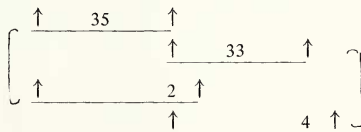
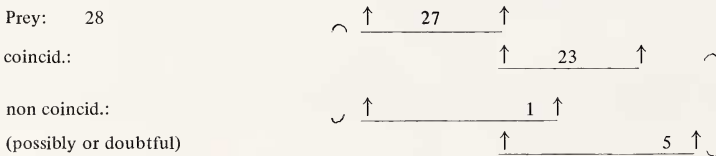


Table 2. (Wasp 1207) Relations between stinging and carrying side of prey (col. 2 and 3) and side where puncture(s) found subsequently (col. 4), including number of punctures (col. 5) and possible effects of chronological order. (Explanations in text). L = left, R = right.

Prey reference number	Observed stinging side	Observed carrying uplifted side	Puncture side	Number of punctures	Puncture coordinates (rf. Fig. 2)	Date (1977)
1	2	3	4	5	6	7
1252		L	L	1	f2(L)	July 16
1253		L	L	1	f2(L)	"
1254	L	L	L	? 1,2	f4(L)	"
1255		R	R	1	f2(R)	"
1261		R	R	1	f3(R)	"
1262		R	R	1	f4(R)	"
1263		R	R	1	f3(R)	"
1264		? L	L	1	g2(L)	"
1284		L	L+R	2	{ g2(L), f3(R)	July 17
1285		R	R	1	g2(R)	"
1286		R	R	1	g3(R)	"
1287		R	R	1	f3(R)	"
1289		L	L	? 1,2	f3(L)	"
1290		R	R	1	f3(R)	"
1303		R	R	1	f3(R)	July 19
1304		R	R	1	f3(R)	"
1306		R	R	?	?	"
1309		R	R	1	g2(R)	"
1310		R	R	? 1 2	g2(R)	"
1311	R	R	R	1	f1(R)	"
1312		L	L	1	g2(L)	"
1313		R	R	? 1,2,3,	{ f3(R), g1(R), f1(R)	"
1318		R	R	1	f1(R)	July 20
1319		R	R	1	f1(R)	"
1320		L	L	1	g2(L)	"
1321		R	R	1	f2(R)	"
1322		L	L	1	g3(L)	"
1323		R	R	1	f2(R)	"

Totals:





and then subsequently re-stung and carried again using the other foreleg base (dropping the prey is not unusual at early hunting stages; see also Steiner 1962, 1976, for *Liris* wasps). In this latter case (b) the coincidence between stinging and carrying sides would still be present. From the data alone it is impossible to decide between a and b. For the six remaining exceptions (1101, 1124, Table 1 and 1254, 1289, 1310, 1313, Table 2), where more than one puncture were found, all stings were on the same side, right or left. Therefore the correlation between side of stinging and carrying was not affected, but it opens the possibility of sting re-insertion for carrying (on the same side) although again two different stinging-carrying episodes, without separate insertion (for paralyzing and stinging), could be involved as well. Furthermore, in all these exceptions, the additional puncture(s) could be abortive sting(s) with incomplete sting penetration (see Steiner 1962, 1976, for such cases in *Liris* wasps). In conclusion, no clear case of discrepancy between side of paralyzing and side of carrying was directly recorded in this study, but the possibility cannot be excluded, on the basis of the data presented.

2. Tables 1 and 2 appear to reveal another curious, unexpected trend: the tendency for identical sting coordinates (col. 6) to appear repeatedly in "runs" of several successive ones (short term constancy in precise sting location), since the data have been presented in exact chronological order, from top to bottom. Thus on Table 1, runs of 3f3, 4g3, 3f2, 3f3 are apparent from top to bottom; in Table 2 similarly, runs of 5f3, 3f1. This could indicate that small behavioural idiosyncracies tend to be maintained over a certain period of time. These runs are not correlated with runs of flies of the same type. These tendencies also apply to the side used for stinging and carrying (col. 3 and 4); unusually long runs involving the same side can be found, particularly in Table 2. However, the total numbers of runs for sides (= r: 19 for Table 1, 12 for Table 2) do not fall outside the ranges of expected randomness for r numbers (12–25 for Table 1; 7–17 for Table 2) at the .05 level of significance, using a runs test (Sokal and Rohlf 1969, p. 624). Furthermore, for wasp 1207 (Table 2) the proportion of sides used (L vs R) is however significantly biased in favor of the right side (R = 19; L = 8;  $X^2 = 4.48$ ;  $df = 1$ ;  $.02 < p < .05$ ) and unbiased for wasp 1019 (Table 1: R = 17; L = 18).

It has not been possible to learn how the wasp frees the prey from the sting, once inside the burrow and/or for prey storage inside the nest cells: does the wasp simply pull the sting inside her abdomen or are the legs also used to push the prey away? Occasionally, for instance when the prey was very big and/or the nest opening or tunnel very narrow, the prey was accidentally released and remained stuck in the entrance while the wasp was continuing her trip, alone, down the tunnel. When this happened, the wasp usually turned around inside the burrow and appeared at the opening head first, grasped the prey with the mandibles (no detailed study of body parts grasped: probably legs or neck) and pulled it inside backwards. This is a typical pompilid (spider wasp) carrying method, believed primitive. Similar behaviour was recorded by Grandi (1961, p. 264), from *O. mandibularis* Dahlbom, by Crèvecoeur (cited by Bischoff 1927), by Masuda (1939, cited by Tsuneki 1969, p. 10), from *O. strandi*, and by Peckham *et al.* (1973, p. 655), from *O. emarginatus*. The latter wasps, however, carry their prey with their legs, mostly midlegs, not on the sting. These wasps therefore did not "re-impale" the fly for prey carrying purpose but used a different method instead. Immediate proximity of the nest opening might be responsible. There is some evidence, however, that under normal circumstances the wasp keeps the fly on the sting once inside the nest, at least for some time, since Tsuneki (1969, p. 6) once opened a nest right after a prey-carrying *O. strandi* had entered it and found the wasp digging in the plugged tunnel with the prey still impaled.

## Experiments

In order to better understand the mechanics of the functional link between prey stinging and carrying, 1) a ciné-photographic analysis was undertaken with a 16 mm Pathé-Webo

camera, using slow motion ciné (64–80 frames/sec) and sequential electronic flash recording, the latter at approximately 1/2000 sec; 2) experimental interruption of prey-carrying and subsequent re-stinging (re-impaling) was obtained by gluing the prey onto the substrate. This method avoided disturbing the wasp by direct intervention (e.g. use of forceps by most authors).

*Results of experiment 1 (ciné-photographic analysis).* – This analysis is summarized in the illustration of this paper. It essentially confirmed the results of direct observation mentioned in the previous section. Unfolding of the previously curled abdomen was revealed in every detail and is shown in Figs. 3A and B and more diagrammatically in Fig. 4a to c. As the wasp uncurled her abdomen, the fly was rotated accordingly and at the end her ventral side faced upwards, with the stinging side tilted upward (Fig. 4c). This had already been reported before, for instance by Ferton (cited in Olberg 1959; see also Ferton 1923, pp. 172–173), but precise analysis requires slow-motion equipment. This behaviour was performed essentially in one of three possible ways, a) the wasp took off at once with the prey (Fig. 5) and rotated the prey in mid-air by straightening up her previously curled abdomen (this is not yet done on Fig. 5); b) the same rotation was done but on the ground, before the wasp flew away with the prey. The wasp usually assumed a tilted posture, more or less “on tiptoe”, and with abdomen lifted (Fig. 3A) so that enough space was available under her body for prey rotation, from dorsum up to venter up (Fig. 4a to c). Figures 3A and 4b show a stage when about half the total rotation of the fly has taken place, while Figs. 3B and 4c show rotation after completion, the left side of the prey (stinging side) being also uplifted. At this point the wasp is ready for her flight to the nest, with the prey impaled; c) during stinging, the wasp had fallen onto her back (venter up) and the fly was on top. In this case, while uncurling her abdomen, after stinging, the wasp also performed a “somersault” that re-established the normal posture (dorsum up) and locomotion and/or taking off could take place as before. After carrying the prey on the wing, the wasp usually landed near or on the burrow entrance (Fig. 3C showing a different prey and carrying side). A study of the wasp abdomen tip at this time reveals that no change of side takes place between take-off and landing. Exceptionally, part of the trip, or the whole trip, was made on foot, by hopping with the help of the wings, particularly when the fly was very large and heavy. After arrival at the nest entrance, the wasp stands on the hind and midlegs, often in a tail erect posture, while the forelegs are used simultaneously for removing the sand plug that closes the burrow (Fig. 3C). Without releasing the fly, the wasp then dives in the opened nest and disappears with the fly.

The longitudinal body axis of the wasp and prey are usually not parallel during carriage in this species, but form a rather open angle (Fig. 2, open arrow; see also Figs. 3B and C and 4c). This reflects the initial stinging direction, during prey paralyzing, which is also slightly tailward (Steiner, in prep.). The large solid arrow on Fig. 2 indicates this average stinging direction and the curved arrow S, the corresponding range of variation. This initial direction tends to be retained during subsequent prey carrying or even exaggerated (more tailward) by the pull. The average prey carrying direction is indicated by an open arrow in Fig. 2 and the corresponding range of variation, greater than for stinging, by the curved arrow C. Therefore the functional link between paralyzing and carrying also includes to some extent the *direction* of sting insertion. The latter was also found to be remarkably constant for *Liris* wasps within each stinging site and was consistent with location of the corresponding ganglion, as also in Fig. 2 (Steiner 1962, 1976). In conclusion, like the “fixed action patterns (FAP’s)” of the ethologists, these activities are much more constant and stereotyped than seems to have been originally assumed on the basis of discrepancies in early reports and/or too limited and superficial observations. Also, the struggle that precedes stinging often conveys the misleading impression that a great variability of stinging postures is involved, with various abdomen insertions. However, a careful study reveals that usually the wasp delivers the final sting only when in the appropriate posture and



Fig. 3(A). Prey-carrying on the sting by the same wasp. Rotation of prey from dorsum up to venter up is about half way completed. Note the "tilted" posture ("on tiptoe") and lifted abdomen of the wasp, that facilitate rotation of the fly under the wasps body. Electronic flash, approximately 1/2000 sec. (also for B to D). (B).Rotation of prey is now complete (prey venter up); the side used for sting insertion (here left side of fly) is higher up than other side. Also note that the wasp abdomen tip is inserted behind the left foreleg of the fly. The longitudinal axes of wasp and prey are not parallel but form an open angle, somewhat variable. (C). The wasp lands on the burrow entrance, with the still impaled prey, and removes the sand plug with both forelegs, while standing on her mid- and hind-legs. Note insertion of sting behind right foreleg and up-lifted right (carrying) side. (D). Ant-carrying *Clypeadon* wasp (*haigi*?) showing insertion of "ant-clamp" in front of midleg bases (both hind and midleg base are visible *behind* insertion point) (S.E. Arizona, summer 1972). In all figures, reference bar = 5 mm.

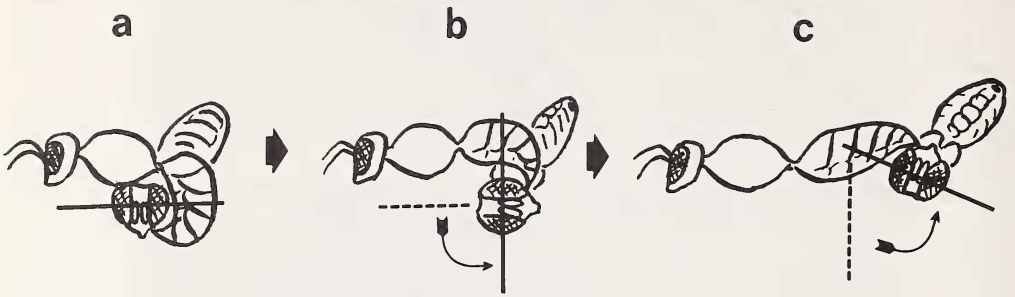


Fig. 4. Diagrammatic representation of prey rotation (from dorsum up in *a* to venter up in *c*), following prey-stinging (in *a*), before prey carrying on the sting, to the nest (*b* shows about half way stage of rotation). Note again in *c* the uplifted stinging/carrying side (left side of prey here) and open angle of wasp/prey longitudinal axes.

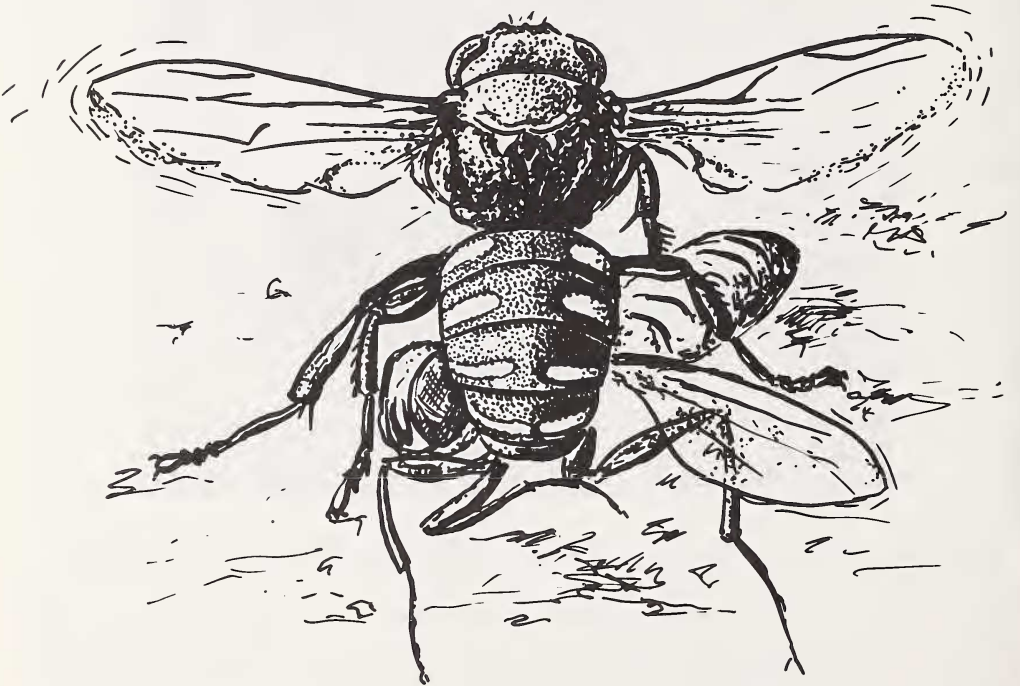


Fig. 5. Taking off with the impaled prey, before rotation of the prey (from dorsum up to venter up) has taken place. The latter is then usually done in flight (sometimes even prey stinging too). Drawn from a somewhat blurred photo, taken with electronic flash at approximately 1/2000 sec.

with the correct abdomen tip insertion behind one foreleg. The latter body site might well be a fixed sign stimulus, in the ethological sense. The same conclusion was reached after the study of some other digger wasps (see Steiner 1976). It also becomes clear that a subsequent study of the puncture(s) left by the sting is indispensable for confirmation of the point really stung. No author appears to have taken this elementary precaution with *Oxybelus* wasps! This pit-fall is even more serious with other digger wasps that do not leave the sting inserted very long. This makes a direct observational recording difficult or impossible and often leads to erroneous conclusions.

*Results of experiment 2 (interruption of transport).*—This experiment was repeated several dozen times with always the same outcome: after the wasp had pulled at the previously stung prey with considerable force, the sting would become de-inserted. The wasp then turned around and re-stung the fly in typical fashion, like in Fig. 1. This might be either re-paralyzing, if venom had been injected, or only sting re-insertion if no venom had been injected, but it was impossible to know. After stinging, the wasp unfolded her abdomen and attempted again to carry away the glued prey. This was often repeated with great persistency, as many as 24 or more times. No observable difference could be detected between the initial stinging (prey paralyzing) and subsequent re-stinging. These observations are also in full agreement with published photos and descriptions of re-stinging (“re-impaling”: e.g. Olberg 1959, p. 378: *O. uniglumis*, and p. 385: *O. argentatus* Curtis; Peckham *et al.* 1973, p. 654).

#### DISCUSSION

Site specificity and constancy of wasp activities on the body of the prey is a fundamental and widespread characteristic of many predatory wasps, and *Oxybelus* wasps are no exception. This applies to body sites used for stinging, egg laying, carrying, malaxation and other prey preparation. Of course the degree of fixity-variability of such activities can vary within considerable limits among species, genera, tribes, etc., and even among activities *within* a species (e.g. *Liris nigra* (Fabricius) wasps, Steiner 1962). Randomness or lack of constancy is, however, clearly the exception. Furthermore, the above even appears to apply in good part to many phytophagous Hymenoptera that often select particular parts of plants for egg laying (e.g. buds, inflorescences, galls, etc.). This body site specificity and constancy could well be and probably is a prerequisite to the ultimate specialization of prey carrying mechanisms mentioned earlier, particularly when it involves precisely adjusted anatomical modifications. Thus Evans (1962a, and b) showed that the ant-clamp of *Clypeadon* wasps is curved downward and fits well the shape of the prey legbases involved (fore- and mid-legbases, Evans 1962b, not mid- and hind-legbases as stated earlier in Evans 1962a). The biconcave pygidium neatly embraces the coxae at the rear and the deeply concave and bilobed hypopygium the coxae in front. Apparently, different *Clypeadon* species prey on different species of ants, and the ant clamp appears to vary accordingly (Evans 1962a, Fig. 4 and 1977). Random insertion of the abdomen tip for carrying and/or for stinging would clearly preclude evolution of such a finely adjusted, highly site specific, organ.

Therefore a functional link between stinging and carrying, as found in some *Oxybelus*, could promote evolution of such an organ. The former ensures a maximum body site specificity and constancy for prey carriage, probably over extensive periods of geological time, judging from its widespread occurrence and stability across genera and even subfamilies. In many cases, stinging site selectivity and constancy are apparently promoted by strong selection pressures such as anatomical characteristics of the prey, location of soft, easily penetrable membranes, by anatomical-physiological characteristics such as location and organization of ganglia controlling locomotion and defense system(s) of the prey (Steiner 1976). As an example, among all

activities of *Liris nigra* wasps, stinging (paralyzing) was found to be by far the most constant and least modifiable one, in terms of body site selectivity and constancy (Steiner 1962). Stinging site specificity and constancy would therefore provide an excellent raw material for opportunistic evolution and consolidation of highly fixed carrying mechanisms like "ant clamps".

A comparative study of this problem in *Oxybelus* species could be very instructive, since this functional link is not found at all in species that never carry the prey on the sting. It is not necessarily present in all "sting-carrying" species, or expressed as consistently. *Oxybelus bipunctatus* is said to impale its prey only after reaching the nest (in Bohart and Menke 1976, p. 366). If so, paralyzing and carrying are distinct activities, at least temporally if not spatially. Even in *O. uniglumis quadrinotatus*, the functional link might not always be as strongly expressed as the present study suggests. Perhaps conditions for more environmentally induced variability were not fulfilled. Also this link might vary individually, regionally, or circumstantially. Thus Peckham *et al.* (1973, p. 652) mention that occasionally a wasp of this species . . . . "carried the prey with her legs to a point near the entrance where, like *bipunctatus*, she impaled it before flying to the nest". But Fig. 4 in the same paper speaks in favor of constancy, since it shows "impaling" by *O. bipunctatus* to be very similar to (probably identical with) the stinging/carrying posture shown on Fig. 1 in the present paper. The apparent placement of the abdomen tip between the fore and midlegs would also be the same. Furthermore, the majority of the clearly readable photos of prey carrying on the sting by various *Oxybelus* species found in Olberg (1959) and Peckham *et al.*, appear to indicate that the wasp abdomen tip is also inserted behind one foreleg of the prey. Therefore constancy within and among *Oxybelus* species might prove much greater than originally believed. Moreover, judging from Nielsen's Fig. 2 (1933, p. 272) the same abdomen tip insertion could apply to *Crossocerus elongatulus* as well as it does to *Oxybelus* and *Clypeadon* wasps (for the latter see also Fig. 3D, present paper).

It would also be interesting to study the prey stinging behaviour of *Clypeadon* wasps in detail, in order to find out if this apparently widespread functional link between prey stinging and carrying a) is still expressed, or b) the prey carrying mechanism has already been "emancipated" from prey stinging, the sting no longer being used for prey holding, although stinging site and carrying might still coincide, or c) carrying evolved independently from stinging and stinging and carrying sites do not coincide. Evans (1962a) states . . . "after they sting the ant, plunging the tip of their abdomen between two pairs of coxae of the ant and fly off to the nest". Later, however, (1962b, p. 473) he says that contrary to earlier statements, . . . "the insertion is *between the front and middle coxae*" (emphasis mine), not middle and hind coxae. This can clearly be seen in Fig. 3D in the present paper. It is precisely again the same insertion site as several *Oxybelus* use for *both* stinging and carrying, and that *Crabro latipes* F. Smith wasps also use for stinging only (Steiner, in prep.). It might therefore well be that stinging by *Clypeadon* also takes place on this site, and that the stinging/carrying link is thus expressed. Furthermore, some other Philanthinae, like *Philanthus triangulum* (Fabricius) also sting their prey behind a foreleg (Tinbergen 1935–1938; Rathmayer 1962, 1978). Even if this is also the case for *Clypeadon*, it would remain to be determined whether or not they also use the sting for holding the prey like *Oxybelus*. Evans (1962a, p. 256) does not think so and points to the fact that the sting is remarkably small and fragile, in contrast to the robust and barbed sting of *Oxybelus* wasps (Evans 1962b, Fig. 4, p. 477) that carry the prey on the sting. Another remarkable similarity can be mentioned: *Oxybelus uniglumis* wasps, like *Clypeadon*, curve the abdomen tip downward while carrying the prey (see Fig. 3A and C). The same is true for several *Crabro* species, which do *not* use the sting. This could be a "precursor of carriage on the sting" (Evans 1962b, p. 478). In summary, "ant clamps" could have evolved from stinging, followed by prey carrying on the sting, as now done by some *Oxybelus*. The abdomen tip of *Oxybelus*

wasps has not (yet?) undergone a modification such that it fits the shape of the point of insertion on the fly's body, like in *Clypeadon*. Considering the great diversity in the flies taken, in sharp contrast to the strict prey specificity found in *Clypeadon* (Evans 1977), this is unlikely to occur, as long as a narrowing of prey selection does not evolve also. (It must also be pointed out that Diptera hunting wasps – and some Hymenoptera-hunting wasps – face a special problem; they cannot easily use the very small antennae of their prey, for carrying, as can many other digger wasps that use prey with large antennae.)

In a previous paper (Steiner 1976) it was argued that evolution of elaborate and rigid prey stinging patterns (e.g. some Orthoptera hunting wasps like *Liris* spp., *Tachysphex* spp., *Prionyx parkeri* Bohart and Menke, *Sphex ichneumoneus* (Linn.), etc.) probably carries with it the "penalty" of some measure of conservatism in prey selection, within rather narrow limits. This also appears to hold for highly rigid and specialized prey carrying mechanisms like the "ant clamp" of *Clypeadon* wasps. Such wasps could easily reach an evolutionary dead end by excessive specialization, if their prey species should happen to disappear. Prey specificity has become extreme in *Clypeadon* while it has remained low in *Oxybelus* wasps, on the whole, and perhaps correlatively the abdomen has remained undifferentiated. Two different evolutionary trends, selection pressures, are perhaps involved, in spite of some similarities.

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